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Preliminary Observations on the Limitations of the Australian Hygrophoraceae (Fungi, Agaricales)

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Abstract

Initial studies of the Australian Hygrophoraceae have demonstrated 57 taxa of which five are also found in Europe, two in North America, nine in New Zealand, with the remaining 41 species so far known only from Australia. Only the genera *Hygrophorus*, *Hygrocybe* and *Camarophyllopsis* are recognised with *Hygrocybe* here including *Bertrandia, Gliophorus, Humidicutis, Camarophyllus* and *Aeruginospora*. *Camarophyllopsis* here includes *Hygrotrama*. The waxy lamellae criterion used for placing species into the Hygrophoraceae is discussed and retained as a valid taxonomic character. The family Hygrophoraceae is retained with tribes Hygrophoreae and Hygrocybeae.

Introduction

Fifty-seven taxa have been recorded during initial studies on the Australian Hygrophoraceae (Young 1996) and the total number for the family in Australia is estimated to lie between 150 and 200 species. Further details of the study methodology, taxa and proposed systematic structure for the Australian species are contained in Young and Wood (1997) but the purpose of this paper is to explore some of the difficulties in deciding whether various fungal taxa should be placed or retained within the Hygrophoraceae, or even whether the Hygrophoraceae should be retained as a useful taxonomic unit within the Agaricales.

Australia has numerous species of genus *Hygrocybe* but relatively few species of other genera within the family Hygrophoraceae. Genera so far undiscovered in Australia include *Hygroaster* and *Neohygrophorus*. This study recognises only one species for each of the genera *Camarophyllopsis* and *Hygrophorus* although more are likely to be assigned to these two genera when the tropical and Tasmanian species are better known. Only seven of the Australian taxa also occur in Europe and North America [e.g. *Hygrocybe cantharellus* (Schwein. : Fr.) Murrill, *H. conica* (Schaeff. : Fr.) P. Kumm. and *H. miniata* (Fr. : Fr.) P. Kumm.] while *H. astatogala* (R. Heim ex R. Heim) Heinem. is also known from Africa. The remainder of the Australian taxa are either indigenous to Australia (41 species) or previously described from New Zealand (9 species) (Horak 1971, 1990).

The validity of the Hygrophoraceae as a natural family within the Agaricales is currently under debate. Horak (1973) described the family as 'a mixture of several heterogenous groups held together by means of more or less unimportant taxonomic characters' and there is no doubt that use of this family (as defined by the characters of waxy lamellae and very long basidia) is being challenged. Both Arnolds (1990) and Bas

(1990) placed the tribes of the Hygrophoraceae within the Tricholomataceae and Bas (1990) stated the intention to propose the latter family for conservation against the earlier name. While their lead has not yet been widely adopted, there is reason to believe that their structure may eventually be found to be correct and the present family Hygrophoraceae of no value other than filing taxa in a convenient pigeon hole.

Studies of the Australian Hygrophoraceae have not resolved the above problems to any great extent, although they do confirm the need for re-appraisal of the validity of the Hygrophoraceae as a natural family and they have shed some light on relationships within its tribes. Because of this fluid situation, the Hygrophoraceae is retained for the Australian taxa while recognising that the family may eventually be discarded as a suitable unit for these taxa. The following discussion considers the limits of the Hygrophoraceae as defined traditionally by the waxy lamellae, the basidial length and the general morphology.

Family Limitations

Waxy Lamellae and Basidial Lengths

The waxy lamellae criterion still remains the critical test for assigning a fungal species to the Hygrophoraceae based on fresh material, and despite its subjective nature, it is still easily distinguished and applied very effectively. If the basidiome has waxy lamellae then they appear translucent, have a brittle texture, and look similar to polished paraffin wax. There is no doubt the character exists despite its unusual nature: the ability to determine a member of the Hygrophoraceae by this test is rapidly learnt by the novice and is reasonably accurate. Once dried, the waxy appearance is lost and herbarium material can be readily assigned to the Tricholomataceae rather than the Hygrophoraceae. Accurate, complete field notes and (if possible) colour images are essential when dealing with herbarium material believed to be within the Hygrophoraceae. Boertmann (1995) similarly commented on the difficulty of identifying dried material suspected to be within the Hygrophoraceae without accurate colour descriptions.

The waxy appearance of the lamellae has been linked to the 'unusual lengths of the basidia' (Singer 1986, Largent 1985), however measurements of basidial mean dimensions for the Australian taxa of this study do not support this concept (Fig. 1). Forty-six of these taxa (82%) have basidia with mean lengths in the interval 24–44 µm; by comparison, taxa of the Tricholomataceae (a family of white spored agarics in which the waxy character is infrequent, and which may be considered to have basidia of 'normal length') have basidia that are generally 20–45 µm, rarely 80 µm. Although one of that family's taxa, *Xerula radicata* (Rehlan : Fr.) Dörfelt (syn. *Oudemansiella radicata* (Rehl. : Fr.) Singer), has very long basidia (70–80 µm), that species as found in Australia does not have waxy lamellae. Further, the greatest basidial length so far recorded for an Australian species of the Hygrophoraceae (59 µm) is far less than that recorded for *X. radicata*.

These results suggest that the basidial length is not the main reason for the waxy appearance of the lamellae which is probably determined by the physical and chemical structures of the basidial wall and possibly also by basidial and hyphal turgor pressure. Cibula (1979) showed that the optical qualities of the pileus of an American species, *Hygrophorus chameleon* Cibula, altered with the amount of water present in the tissues and there is tentative support for the turgor pressure concept. Many Australian species of the Hygrophoraceae have very thin hyphal walls and the high water content of the fungal basidiome has already been noted (Arnolds 1981). High turgor pressure and

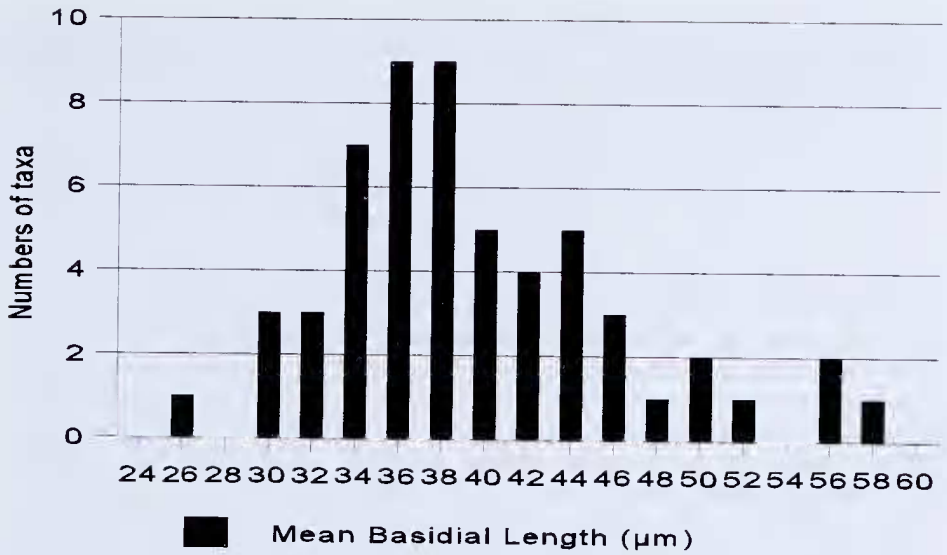

Fig. 1. Numbers of taxa of the Australian Hygrophoraceae according to each taxon's basidial mean length; interval 2 µm.

water content coupled with the thin hyphal walls, already observed as a character in this family, could account for the brittle nature of the lamellae, while the high turgor pressure is suggested by the tendency of some species to 'weep' watery latex from the tissues when cut.

Morphological Comparisons with Other Taxa

(a) Family Tricholomataceae and the Hygrophoraceae

The Tricholomataceae is the closest family to the Hygrophoraceae. An inspection of Singer's (1986) definitions of the two families shows so much similarity between the two sets of characters, that the presence of waxy lamellae becomes the criterion for separation of the two families. Australian data appears to confirm this family proximity for it shows that the mean basidial lengths of the taxa of the Australian Hygrophoraceae are similar to those of the Tricholomataceae and members of the two families are separated only by the waxy lamellae character. Since European species also showed this similarity, Arnolds (1990) placed tribes Hygrocybeae and Hygrophoreae in the Tricholomataceae. This combination is still to be completly accepted (e.g. Hansen and Knudsen 1992) and it is not applied in this study. It is important to note that when defining generic limits, the genera whose species are most likely to be confused with those of the Hygrophoraceae are all within the Tricholomataceae: *Mycena, Hemimycena*, *Dermoloma*, *Omphalina*, *Gerronema*, *Clitocybe*, *Porpoloma*, and *Omphaliaster.*

Within the Hygrophoraceae the tribe Hygrophoreae is well defined by the presence of a divergent hymenophoral trama. Genus Hygroaster (tribe Hygrocybeae) approaches this divergent structure at the sides of the trama but differs by being irregular at the centre (Singer 1986). Since tribe Hygrophoreae combines the divergent trama with a filamentous pileipellis, broadly adnate to decurrent lamellae, a frequently occurring viscid universal veil and a mycorrhizal habit, the tribe forms a very natural group of taxa within the Hygrophoraceae. (Divergent tramas do occur in other white spored genera,

e.g. *Amanita*, but other characters present clearly separate those taxa from the Hygrophoraceae.) The sole Australian taxon currently ascribed to the Hygrophoreae, *Hygrophorus involutus* G. Stev., can only be accorded provisional membership until the trama of fresh material can be examined.

For tribe Hygrocybeae, only the genera *Hygrocybe* and *Camarophyllopsis* have been recorded for Australia. Provided the waxy lamellae character is apparent, *Camarophyllopsis* is defined by its hymenidermic pileipellis, often decurrent lamellae and dull colours in greys or browns. The genus *Hygrocybe* is more difficult to define as the species within the genus have characters that are more varied. If the basidiomes are large, brightly coloured and exhibit waxy lamellae, little difficulty is experienced; most problems occur when the basidiomes are small, dull coloured and the normally distinctive features of the family may be overlooked, a point also made by Hesler and Smith (1963). Frequently, the species are assigned to genus *Hygrocybe* on a group of characters taken together, rather than a single definitive character. For example, species within *Hygrocybe* generally have lamellae that are distant and thick in addition to their waxy appearance, and their habit of growing on mossy soil or humus is an additional ecological character that may be used. At the microscopic level, hymenophoral trama and pileipellis structures are extremely useful, but additionally, the thin hyphal walls and the presence or absence of clamps, together with clamp structure, can be added to the overall character assemblage. Subgenus *Hygrocybe* is well defined by the very long, aseptate, tubular elements of the lamellae trama. Although there are some members in which the elements are shorter, the lack of tramal clamps, the presence of lactifers and the conical, often brightly coloured, radially splitting pilei are very distinctive and permit their easy recognition. No Australian taxon has been found which is intermediate between subgenera *Hygrocybe* and *Pseudohygrocybe*, nor has a member of the Tricholomataceae been encountered where the lamellae trama contain tubular elements similar to those in subgenus *Hygrocybe*.

(b) Genus Mycena

Most problems of delimitation against other genera occur within subgenus *Pseudohygrocybe* because the variations at the limits of sectional ranges can be extreme. *Gliophorus pallidus* E. Horak, which belongs in this subgenus, might be confused with some small, whitish and glutinous taxa of *Mycena* such as *Mycena austrororida* Singer, however the amploid spores of that species — abundant and sinuous cheilocystidia, cellulodermic pileipellis and caespitose habit on wood — immediately distinguish it. Taxa of *Mycena* are usually readily identified when several of its defining characters are apparent: amyloid spores, diverticulate hyphae in the pileipellis, pileocystidia and abundant and varied cheilocystidia. Other useful characters are the presence of pleurocystidia or (when it occurs) a lignicolous substrate (logs, twigs or branches in forest litter). Where the hyphae of the pileipellis are not diverticulate, they may be globose (as in *Mycena austrororida*) or smooth but in these taxa other characters typical of the genus will be present. Again, it is the lack of these fundamental characters that so often characterises the Hygrophoraceae.

(c) Genus Hemimycena

Hemimycena is closely related to *Mycena*. It comprises mostly small, white and delicate taxa which in the past have been mistakenly placed in *Hygrocybe*. Arnolds (1985) described the species *Hygrocybe griseopallida*, but later synonomised this with *Hemimycena mairei* (E.J. Gilb.) Singer after re-examination revealed the characteristic diverticulate hyphae in the pileipellis. The sub-regular trama and decurrent lamellae in

Hemimycena suggest subgenus *Cuphophyllus*, but the diverticulate hyphae usually present in the pileipellis, the cheilocystidia and pleurocystidia usually present and the extremely small basidiomes that are gregarious on litter all serve to separate the genus. *Hemimycena* is not yet known for Australia but it is present in New Zealand (Horak and Desjardin 1994). This fact, together with the abundance of small, white agarics in Australian tropical and temperate rainforests, suggests Australian species of *Hemimycena* will be found.

(d) Genus Clitocybe

The genus *Clitocybe* and its relationships to other genera have been extensively discussed (Bigelow 1982; Singer 1975, 1986) and only *Hygroaster* was suggested as having any delimitation difficulties with *Clitocybe*, however the unique trama and the stellate spores of Hygroaster separate it immediately. Only taxa in subgenus *Cuphophyllus* (subdued colours and decurrent lamellae) might be confused with *Clitocybe*, however the thick, widely spaced lamellae of the Hygrophoraceae bear little resemblance to the narrow, crowded lamellae found in *Clitocybe*. Species of *Cupophyllus* are also separated by the more robust basidiomes of *Clitocybe*. Basidiomes of *Pseudohygrocybe* which approach the overall morphology of *Clitocybe* are also readily separated from *Clitocybe* because they are either highly glutinous with either (or both) cheilocystidia and caulocystidia (unknown in *Clitocybe*) or are highly coloured in reds, oranges or greens. Such colours are generally absent from *Clitocybe*. No Australian taxa are yet known which would cause difficulties in separating a species of *Clitocybe* from the Hygrophoraceae.

(e) Genera Gerronema *and* Omphalina

Two genera of the Tricholomataceae, *Gerronema* and *Omphalina*, are separated from each other by their different pigmentation structures in the pileipellis (Singer 1975, 1986). The bright pigments present in certain small taxa within these two genera initially suggest the species *Hygrocybe cantharellus* because they display the decurrent lamellae and habit of that taxon. Separation is usually on a group of characters not present in one or other of the genera. Basidiomes of *Omphalina* and *Gerronema* are always quite small, dry and invariably have decurrent lamellae. When semi-decayed logs form the substrate for the basidiome, *Gerronema* and *Omphalina* are indicated while *Hygrocybe* is virtually eliminated. Similarly the presence of abundant, bristling cystidia especially where they occur on the pilcal surface is also an indicator of the Tricholomataceae since such structures are not present in the Hygrophoraceae. Spores in *Omphalina* and *Gerronema* tend towards cylindric or tilda (~) shapes, rather than the ovoid to globose shapes in the Hygrophoraceae, and the trama is always irregular (or if regular, then only at the very centre with the sides irregular) while the taxa close to *H. cantharellus* have regular tramas. Arnolds (1985) discussed the omphaloid taxon *Hygrocybe viola* J. Geesink & Bas and noted its apparent proximity to *Omphalina*. He considered it well separated because of its intracellular or parietal pigments rather than strongly encrusting pigments found on the hyphae of the pileipellis, the presence of medallion clamps and lactifers, and the long basidia rather than the shorter basidia found in *Omphalina* and taxa close to *Omphalina*. Medallion clamps are absent from *Omphalina* (Arnolds 1986), but they occur extensively in the Hygrophoraceae. The presence of encrusting pigment on the cuticular hyphae would also serve to separate species of *Hygrocybe* as the taxa around *H. cantharellus* have intracellular pigments. Although the lamellae in *Omphalina* and *Gerronema* may be thick and decurrent, they are never waxy in appearance.

(f) Genus Dermoloma

The genus *Dermoloma* (J.E. Lange) Singer has been variously placed in the Hygrophoraceae and the Tricholomataceae. Arnolds (1990) placed it in the Tricholomateae *sensu* Arnolds; Arnolds (1992) revised his position and argued that the genus should be placed within the Hygrocybeae. Singer (1975, 1986) has consistently maintained its position in the Tricholomataceae, a position also taken by Pegler (1983, 1986) and Hansen and Knudsen (1992). Corner (1994) discussed the Malesian species of *Dermoloma* at length and with reference to the European taxon *D. cuneifolium* (Fr. : Fr.) Bon, the taxon upon which Arnolds (1992) based his assumptions. Corner found that the amyloid spore character in *D. cuneifolium* is extremely variable in basidiomes growing side by side, some being amyloid and others inamyloid. Corner also noted that the characters present in the 13 Malesian species referrable to *Dermoloma* 'so extended the idea of the genus ... [that they] ... nullify its use.' On the basis of his investigations, Corner reduced *Dermoloma* to synonymy with *Tricholoma* (Fr.) Staude and hence placed the Malesian taxa within the Tricholomataceae.

Assuming the genus is retained, *Dermoloma* seems close to *Camarophyllopsis*, but the holotype species, *D. cuneifolium* (Fr. : Fr.) Bon has very short basidia (mean 26.5 x 6.3 μm) while the sole Australian taxon so far known for *Camarophyllopsis* has basidia with a mean of 40 x 6.7 μm. The spores also differ: in *Dermoloma* they are usually elliptical although they may approach subglobose and they may be amyloid; in *Camarophyllopsis* they are generally distinctly subglobose and inamyloid. The pileipellis also differs: species of *Camarophyllus* have an hymenoderm (which may be reduced to a layer of pyriform to more or less globose elements) rather than the densely packed regular cutis of *Dermoloma*. The position of *Dermoloma* thus remains controversial with very different family relationships proposed. While it is agreed that *Dermoloma* does approach *Camarophyllopsis*, the two genera are here retained in separate families (or tribes) until more conclusive evidence is produced.

(g) Genus Porpoloma

Porpoloma Singer presents similar problems to those of *Dermoloma*. During the study of the Hygrophoraceae, material was collected of an undescribed taxon in the Bunya Mountains (Queensland) which on field characters was at first assigned to the brown pigmented group of taxa within *Pseudohygrocybe*. The strong amyloid reaction of the spores and basidial length (mean 36.5 x 7 μm), indicated the genus *Porpoloma*. Singer (1975, 1986) also agreed that *Porpoloma* approached the brown group of taxa within *Hygrocybe* but considered that the short basidia and amyloid spores were sufficient to separate them. Whilst the amyloid spore argument is still undoubtedly valid, the basidial length criterion is not. The only taxon with amyloid spores widely accepted as being in the Hygrophoraceae and apparently close to subgenus *Cuphophyllus* is *Neohygrophorus angelesianus* (A.H. Sm. & Hesler) Singer with its irregular trama, decurrent lamellae and intracellular cuticular pigments. Singer (1962) detailed his studies of the holotype to see if it could be moved to the Tricholomataceae but the long basidia, the waxy lamellae and the obvious proximity to *Cuphophyllus* convinced him that it was correctly retained in the Hygrophoraceae. Singer maintained this position in all future publications. The intense amyloid spore reaction in *Porpoloma* together with its 'hygrophoraceous' macrocharacters make family allocation of this taxon difficult to resolve, but the amyloid reaction seems sufficient to separate it from the brown pigmented taxa within the Hygrophoraceae.

(h) Genus Omphaliaster

Most authors do not consider *Omphaliaster* to be within the Hygrophoraceae and Bas (1990) placed the genus in Tribe *Clitocybe* with *Omphalina*. Hansen and Knudsen (1992) retained *Omphaliaster* in the Tricholomataceae, while Moser and Jülich (1988) also placed *Omphaliaster* outside the Hygrophoraceae. Singer (1975, 1986) regarded *Omphaliaster* as a synonym of *Hygroaster* but the analysis by Baroni (1982) is very clear and leaves no doubt that *Omphaliaster* is quite separate from *Hygroaster* on the basis of hymenial structure and pileal pigmentation. The separation of *Omphaliaster* from subgenus *Cuphophyllus* is defined on a group of characters rather than a single one: the habit of *Omphaliaster* is omphaloid and is somewhat similar to those genera that fit within subgenus *Cuphophyllus*, however species of *Omphaliaster* have a regular to sub-regular trama in the lamellae rather than the irregular trama in *Cuphophyllus*, have lamellae faces with abundant pseudocystidia which are absent in *Cuphophyllus* and frequently have encrusted pigments in the pileipellis while the pigments are intracellular in *Cuphophyllus*. Dennis (1953) and Pegler (1983) describe the waxy nature of the lamellae of *Hygroaster* but there is no suggestion of the same waxy nature in the lamellae of *Omphaliaster*.

Conclusions

Despite the apparent similarity between the Tricholomataceae and the Hygrophoraceae, on balance, it is argued that as far as the known Australian taxa of the Hygrocybeae are concerned, the two families should not yet be combined. The waxy character of the Hygrocybeae is likely to be caused by physical and chemical factors within the basidiome which do not seem to occur widely in the Tricholomataceae and it is so distinctive and consistent in these taxa that it does define a unique species aggregate within the Agaricales. With the waxy character come a series of supporting characters for many species (bright colours, extremely watery context, tramal and pileipellis structures etc.) that add weight to the separation. Only a single taxon within the Hygrophoreae is partially known for Australia and its possible relationships to the Tricholomataceae or the Hygrocybeae remain uncertain.

Family Tricholomataceae is already a very large, complex aggregate of white spored species. The transfer of the tribes of the Hygrophoraceae into the Tricholomataceae has some merit as far as morphology is concerned, but it does not resolve the questions of why these waxy gilled taxa have their peculiar physical characteristics and whether their origins are similar to those of the Tricholomataceae. Resolution of the Hygrophoraceae and Tricholomataceae problem will probably remain until comprehensive genetic studies are completed, but despite the present use of a separate Hygrophoraceae, it would not be a surprise to discover that at least the Hygrophoreae (and possibly also the Hygrocybeae) should be placed within the Tricholomataceae.

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